

TWO MORE SIBLING SPECIES OF ALPHEID SHRIMPS ASSOCIATED WITH THE CARIBBEAN SEA ANEMONES *BARTHOLOMEA ANNULATA* AND *HETERACTIS LUCIDA*

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ABSTRACT

We have described two new species of snapping shrimp, *Alpheus polystictus* and *A. roquensis*. The new species form part of a complex of four sibling species associated with Caribbean sea anemones, the others being the well-known *A. armatus* Rathbun, 1900 and the recently described *A. immaculatus* Knowlton and Keller, 1983. *Alpheus roquensis* is found with the anemone *Heteractis lucida*, while the other three shrimps live with *Bartholomea annulata*. In laboratory choice experiments, each shrimp species prefers the species of anemone with which it is typically found in the field, although each can shelter under the other species of anemone. All four species are extremely similar morphologically, being distinguished largely on the basis of color pattern. The validity of the species is confirmed by the total absence of interbreeding; heterospecific male-female pairs are never found in the field, and it is impossible to force pairings between species in the laboratory. *Alpheus polystictus* is rare in Jamaica and Haiti, while in Venezuela it is sometimes the dominant species to depths of 10 m. In the areas examined, it has always occurred with at least one of the other two *Bartholomea* associates. The geographic distribution of *A. roquensis* is more limited, as there are no reports of alpheidids associated with *Heteractis lucida*, and none has been found with this anemone in Jamaica.

The Caribbean sea anemone *Bartholomea annulata* (Lesueur) has long been known to shelter alpheid shrimp; a single juvenile shrimp is often found with small anemones, while a male and a female typically occupy larger anemones or clusters of contiguous anemones (Limbaugh et al., 1961; Chace, 1972; Smith, 1977; Knowlton, 1980). Until recently it was assumed that all of these alpheidids belonged to the same species, *Alpheus armatus* Rathbun. Detailed ecological and behavioral study (Knowlton, 1978; 1980) revealed, however, the presence of several "morphs" which mate in a strictly assortative manner and must therefore be considered separate species. We earlier described *A. immaculatus* Knowlton and Keller, 1983, the other common species in Jamaica. Here we describe a third *Bartholomea* associate, *A. polystictus*, which is rare in Jamaica and Haiti but abundant in Venezuela.

The anemone *Heteractis lucida* Duchassaing and Michelotti has not previously been reported as having alpheid symbionts (Colin, 1978). Most individuals around the island of Dos Mosquises, Los Roques, Venezuela, however, were found to shelter one or two alpheid shrimp very similar to but distinct from the other three species of anemone-living alpheidids. This fourth species, *A. roquensis*, is also described below.

Finally, we summarize the differences in color, morphology, and ecology among the four species, and present experimental data on pairing behavior and host preference.

METHODS AND MATERIALS

The data reported below derive largely from shrimp collected in Venezuela during 1983 and 1984; measurements of specimens collected in Jamaica (1981-1983) and Haiti (1981) are also included. All measurements except total length were made using an ocular graticule.

Behavioral experiments were done at the Estación de Biología Marina Dos Mosquises, Los Roques, Venezuela, during the summer of 1984. To compare intra- and interspecific pairing, a shrimp was placed in a tank with a monospecific cluster of anemones in the afternoon, and a potential mate was placed in the tank in the evening. The following morning the locations of the two shrimp were noted (separate vs. together), and both shrimp were examined for injuries. Usually the female was the initial resident, and had a greater total length but a smaller claw size than the subsequently introduced male (the typical field situation; Knowlton, 1980). Only sexually mature shrimp were used (males 24 to 40 mm and females 27 to 50.5 mm in total length). All intraspecific combinations and those interspecific combinations involving *A. roquensis* were performed with both *B. annulata* and *H. lucida*. In host-preference experiments, aquaria with the two species of anemones located at opposite ends were used. A shrimp was introduced to one of the two species in the evening, and its position was noted the following morning. In these experiments most individuals were sexually mature adults, although some juveniles were tested (minimum size 11.5 mm total length). For both pairing and host preference experiments, the sizes of the aquaria and the anemone clusters were varied to match the size of the shrimp, and no individual was used more than once per experiment.

Alpheus polystictus new species

Material Examined.—Morrocoy, Venezuela (−1 to −10 m): 6 males (including holotype USNM H-216783), 5 females, 1 juvenile; Los Roques, Venezuela (−1 to −5 m): 18 males, 18 females; Discovery Bay, Jamaica (−3 to −12 m): 4 males, 7 females, 1 juvenile; Caracol Bay, Haiti (−1 m): 1 male. Mate of holotype deposited at the National Museum of Natural History (USA) as paratype.

Description.—In general this species is very similar to *A. armatus* and *A. immaculatus*. For a detailed and figured description of the latter see Knowlton and Keller (1983). Below are summarized the most important features.

Rostrum extending to about anterior margin of basal segment of antennular peduncle; somewhat depressed. Ocular hoods mesially delimited by adrostral furrows; armed with sharp dorsomesial tooth. Variably shaped tooth on midline of carapace about even with base of ocular hoods. Carapace smooth, laterally compressed; posterior margin with cardiac notch.

Abdominal somites smooth. Telson about two-thirds as wide as long with two pairs of dorsal spines; posterior margin with two pairs of lateral spines.

Eyes completely enclosed within ocular hoods.

Antennular peduncle extending slightly beyond antennal scale; stylocerite sharply acute, extending nearly to end of first segment of antennular peduncle; second segment somewhat longer than first and at least twice as long as third. Lower flagellum about three times longer than upper flagellum, extending to or beyond posterior margin of carapace.

Antennal scale about four times as long as wide; narrow slit extending antero-laterally along distal half, partially separating outer spine from inner lamina. Antennal peduncle extending beyond antennular peduncle; basal segment armed with sharp ventrolateral tooth; distal segment slender, with well developed flagellum extending posteriorly far past telson.

Third maxilliped extending nearly to tip of antennal peduncle.

Major first pereopod overreaching antennal peduncle by much of chela. Chela compressed, ovate, twisted, with fingers closing in plane nearly perpendicular to plane of compression of proximal part of palm; proportionately larger in adult males than adult females. Fingers typically less than half length of palm; opposing margin of fixed finger with small blunt tooth distal to socket into which large flattened tooth of movable finger fits. Palm with numerous tubercles and long setae on surface which grades into fixed finger; sharp marginal tooth adjacent to insertion of movable finger; paired, weakly developed tuberculous ridges on both sides of palm along plane of compression; surface from which movable finger extends smooth with small blunt tooth adjacent to insertion of movable finger. Merus with sharp distal tooth, flexor margins weakly denticulate.

Minor first pereopod extending beyond antennal peduncle by most of chela. Fingers somewhat longer than or subequal to palm; movable finger with row of small teeth which oppose blade-like ridge on fixed finger. In large males (>16–26 mm total length) movable finger somewhat “balaeniceps shaped” (Banner and Banner, 1966, p. 17); row of coarse, short setae extending over proximal half of fixed finger to either side of blade-like ridge. Palm subcylindrical; surface from which movable finger extends smooth, opposite surface tuberculose with long setae; acute teeth dorsal (well-produced) and ventral (less-produced) adjacent to insertion of movable finger. Carpus with tooth on distal extensor margin. Merus with sharp distal tooth, flexor margins weakly denticulate; longer than merus of major cheliped and subequal in width.

Second pereopod extending past antennal peduncle by at least length of chela and most of carpus; fingers subequal in length to palm; carpus about four times longer than chela with five articles ($1 \text{ (proximal)} \gg 2 \geq 5 > 3 \geq 4$); merus somewhat longer than proximal article of carpus and subequal to or longer than ischium. Third pereopod overreaching antennal peduncle by dactyl and much of propodus; dactyl simple, unarmed, and about one-fourth length of propodus; propodus with two distal spines flanking dactyl insertion and series of spines along flexor margin; carpus about two-thirds length of propodus; merus about twice as long as carpus and armed with acute tooth distally at flexor margin; ischium armed on lower face with sharp, movable spine. Fourth pereopod extending past antennal peduncle by dactyl and part of propodus, similar to third pereopod except slightly fewer propodal spines. Fifth pereopod somewhat smaller than third and fourth, overreaching antennal scale by dactyl; propodus with spines on flexor margin, pair of spines at dactyl insertion, and dense tuft of short setae on distal fourth; merus and ischium unarmed.

Second to fifth pleopods similar in size. Appendix masculina on second pleopod of adult males shorter than or subequal to appendix interna.

Uropods subequal in length and somewhat longer than telson; lateral branch with tri-lobed transverse suture near distal margin, long slender spine inserting between two acute teeth at lateral end of suture; mesial branch unarmed.

Color in Life.—Juveniles and adults have red-and-white banded antennal flagella. The body of adults has a complex pattern of translucent, white, and dark red or purplish-red patches (Fig. 1). There are dark, eye-like markings on the sides of the second and third abdominal somites. The sixth abdominal somite is bluer than the more anterior somites in individuals less than 17 mm total length. The most distinctive feature is a profusion of small, iridescent greenish (chartreuse) spots. They are abundantly scattered over both sides of the first pair of claws, the third pair of maxillipeds, the antennal peduncle and scale, and the antennular peduncle, and they occur along the dorsal midline of the carapace and abdomen. There are often some spots on the middle pereopods, the pleopods, and on the sides of the last three abdominal somites. There is almost always at least one spot on each of the inner uropods, and there may often be multiple spots on both these and the sides of the telson itself. On the appendages these green spots lie within larger translucent patches which are particularly conspicuous on the major and minor chelae. Finally, the spines on the outer uropods are typically dark brown on males and medium brown on females, although both sexes show considerable variability in the intensity of spine pigmentation, ranging from light brown to black.

Measurements (in mm).—Total length: males 15 to 43.5 (holotype 33.5), females 13 to 50.5, juveniles 5 and 6.5. Carapace length: males 5 to 14 (holotype 11.5),

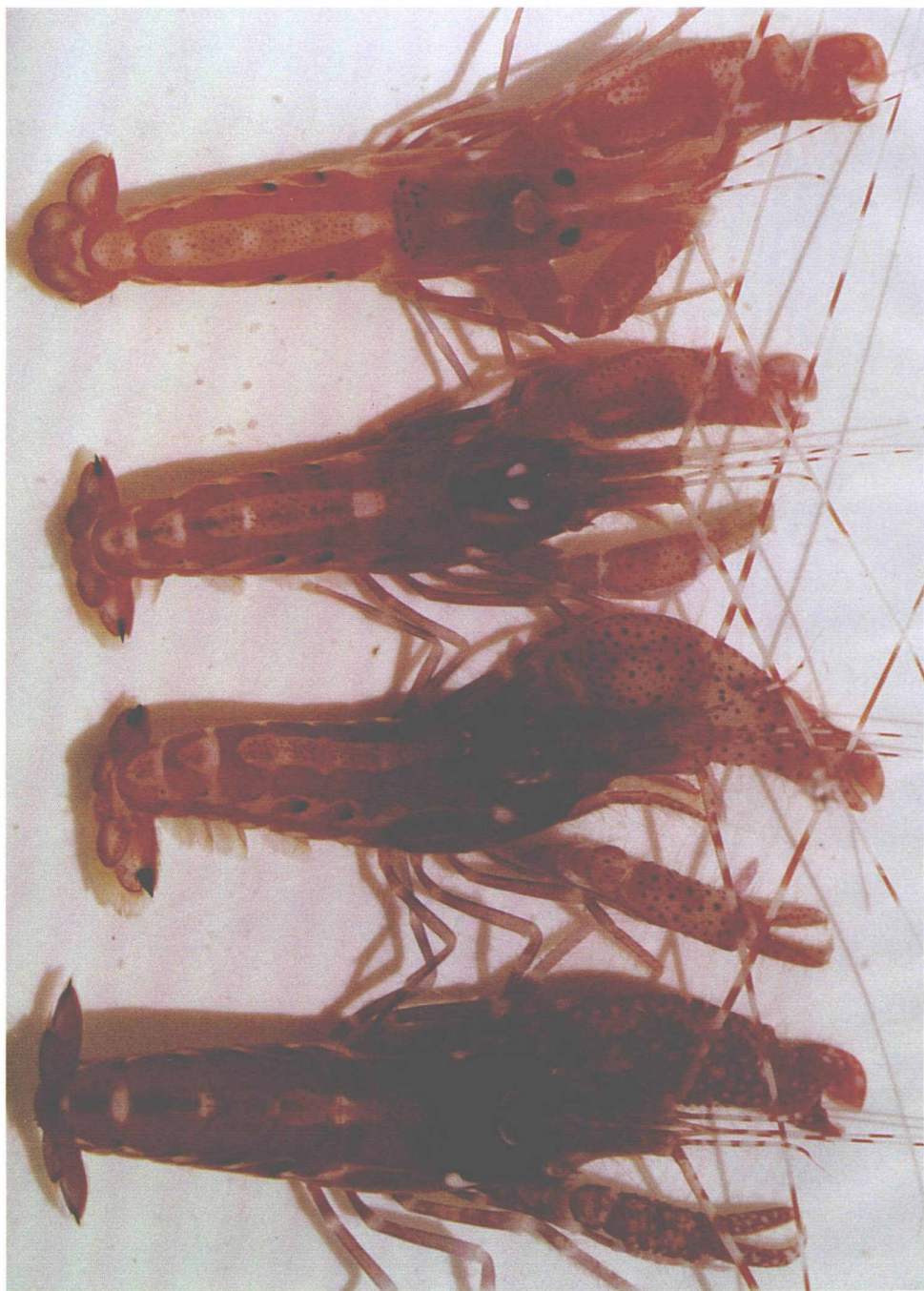


Figure 1. The four alpheid symbionts. All are males between 30 and 34 mm in total length, collected in Los Roques, Venezuela. From top to bottom they are *A. immaculatus*, *A. armatus*, *A. roquensis* and *A. polystictus*. In addition to the overall similarity in color pattern, note the differences in uropod spines, the many, small translucent-white patches on the chelae of *A. polystictus*, and the especially conspicuous red tubercles on the chelae of *A. roquensis*. The green spots are not visible.

females, 4.5 to 16.5, juveniles 1.5 and 2. Length of propodus of major first pereopod: males 7 to 25 (holotype 18.5), females 5 to 21, juveniles 1.5 and 3.

Habitat.—This species has always been found associated with the sea anemone *Bartholomea annulata*. Adults live in male-female pairs with large anemones or anemone clusters, while juveniles live singly with smaller anemones.

Type Locality.—Morrocoy, Venezuela (Isla Sombrero, -2 m), from the anemone *Bartholomea annulata*.

Distribution.—Probably throughout the West Indies and the Caribbean region. It has been observed in Jamaica, Haiti, Panama, and Venezuela, and appears to be more common in the southern Caribbean (e.g., 10 of 13 pairs and 28 of 41 individuals noted in Venezuela, vs. 0 of 9 pairs and 1 of 37 individuals noted in Haiti).

Etymology.—The name "polystictus" is taken from the Greek for "much-spotted," referring to the multitude of greenish spots which unambiguously distinguish the species when alive.

Alpheus roquensis new species

Material Examined.—Los Roques, Venezuela (-3 to -16 m): 18 males (including holotype USNM H-216785), 13 females. Mate of holotype deposited at NMNH (USA) as paratype.

Description.—This species differs very little from the description provided above for *A. polystictus*. The only conspicuous difference is that the tooth on the midline of the carapace even with the base of the ocular hoods is typically very reduced and sometimes entirely absent. (Quantitative comparisons of this and other morphological differences among the four species are presented in a following section.)

Color in Life.—The general color pattern is very similar to that of *A. polystictus* (Fig. 1). The major differences are that the antennal flagella of juveniles have few or no red bands, the sixth abdominal somite is not distinctly bluish, the body in general is not as deeply pigmented, the uropod spines are usually red in females and black in males, and the green spots are not nearly as numerous or widespread. The last feature is particularly evident for the claws, where the spots are not individually surrounded by translucent patches and occur only on the inner faces in irregular clusters. (A summary of color differences among the four species is presented in a following section.)

Measurements (in mm).—Total length: males 15 to 33.5 (holotype 27), females 8.5 to 37. Carapace length: males 5 to 11 (holotype 8.5), females 3 to 12.5. Length of propodus of major first pereopod: males 6.5 to 21.5 (holotype 17.5), females 3 to 18.5.

Habitat.—*Alpheus roquensis* is almost always associated with the sea anemone *Heteractis lucida*, although we once found an individual with *Bartholomea annulata* in an area where *Heteractis* was not abundant. As in the other three species, pairs of reproductive adults are found with large anemones or anemone clusters, while juveniles live singly with smaller anemones.

Type Locality.—Los Roques, Venezuela (Isla Dos Mosquises, -9 m), from the anemone *Heteractis lucida*.

Distribution.—This species has only been collected or seen off the islands of Dos Mosquises and Cayo Sal in the Los Roques Archipelago off the coast of Venezuela.

Table 1. Color differences among the four species. "Spots" refer to green-gold markings, "stripe" to translucent band down midline, "patches" to translucent-white areas, and "tubercles" to raised, pigmented markings

Character	<i>A. polystictus</i>	<i>A. roquensis</i>	<i>A. armatus</i>	<i>A. immaculatus</i>
Uropod spots	present	present	absent	absent
Maxilliped spots	many	few	none	none
Outer chela spots	many	none	none	none
Inner chela spots	many, scattered	some, clusters	some, linear	none
Juvenile antenna	banded	few or no bands	banded	no bands
Egg color	dark red	red	red	olive
Male uropod spines	dark brown	black	black	red
Female uropod spines	brown	red	red	red
Juvenile 6th somite	blue	not blue	not blue	not blue
Adult carapace stripe	absent	absent	often reduced	present
Inner chela patches	many, small	few, large	few, large	few, large
Red chela tubercles	inconspicuous	very conspicuous	conspicuous	conspicuous

Papers which mention the association of *A. armatus* with *Bartholomea* make no explicit mention of alpheidids with *Heteractis* (Limbaugh et al., 1961; Chace, 1972; Mahnken, 1972; Herrnkind et al., 1976; Colin, 1978; Criales, 1984), although some of these papers either fail to mention *Heteractis* or do not specify the identity of other anemone species from which alpheidids have occasionally been collected. Colin (1978, p. 187) states that commensal crustaceans are only rarely found with *Heteractis*, and we found no alpheidids during a search of 99 *Heteractis* in backreef and forereef environments (–2 to –15 m) near Discovery Bay, Jamaica (areas where 20 of 39 *Bartholomea* sheltered alpheidids). The proportion of *Heteractis* occupied by alpheidids in Los Roques is so high (87%, N = 131) that we doubt whether such a situation would be reported by others as an occasional or unusual association. It thus seems likely that the geographical distribution of this species is more limited than the distributions of the other three species.

Etymology.—The name "roquensis" comes from the archipelago, Los Roques, where the species was discovered.

Comparisons and Interactions among the Four Sibling Species

Distinguishing Features in Color Pattern, Morphology and Ecology.—Bruce (1975) has noted that many species of shrimp have consistent color patterns which sometimes provide the most reliable characters available for the identification of living individuals. This is definitely true for *Alpheus armatus*, *A. immaculatus*, *A. polystictus*, and *A. roquensis* (Table 1). Most useful are the greenish spots, particularly on the chelae and uropods, which can be used to identify all but the most recently settled individuals (i.e., total length <6 mm). The four species can be arranged in a series with respect to number and patterning of these spots: *A. polystictus* has the most numerous and widespread spots, while *A. immaculatus* has none; *A. roquensis* falls between *A. polystictus* and *A. armatus* in both number and position of spots. Small juveniles, which have many fewer spots, can still be distinguished by noting the presence or absence of green spots on the uropods and red bands on the antennae. Unfortunately, the green spots disappear soon after preservation. Other characters, such as antennal banding, the patterning of translucent areas, and uropod spine color, can be assessed in more recently preserved individuals.

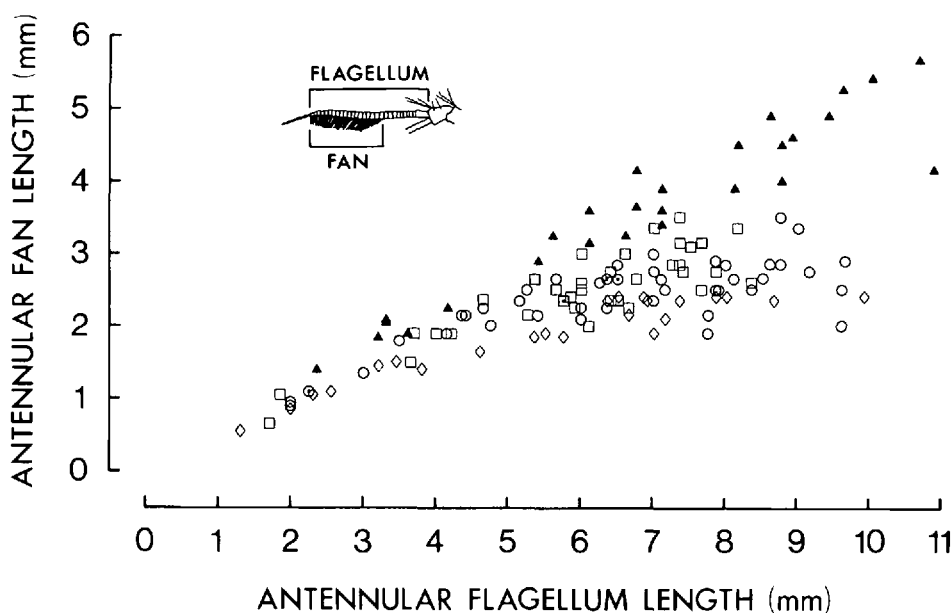


Figure 2. Relative length of right antennular fan. *Alpheus polystictus* (solid triangles) is sufficiently different from the other three species (open symbols: circles—*A. armatus*, squares—*A. immaculatus*, diamonds—*A. roquensis*) in this character to aid in the identification of individual specimens.

Clear-cut morphological differences are less evident. Knowlton and Keller (1983, fig. 5) found little overlap in the shape of the rostrum between adult *A. armatus* and *A. immaculatus*. This continues to be a good morphological character for *A. immaculatus*, because *A. polystictus* and *A. roquensis* do not differ from *A. armatus* in this regard. *Alpheus polystictus* is most distinctive morphologically in the relative length of the fan of setae on the lateral antennular flagellum (Fig. 2). *Alpheus roquensis* differs in having a relatively small or absent tooth posterior to the rostrum at the level of the base of the ocular hoods (Fig. 3). Males of this species are also unusual in often having proportionately wider uropod spines (Fig. 4), and in having enormous variability in the relative length of the spine (Fig. 5). Males of *A. armatus* have relatively longer spines than *A. immaculatus* or *A. polystictus* (Fig. 5), and can also be distinguished from males of *A. roquensis*, whose spines are proportionately wider (Fig. 4).

These characters are useful but not foolproof in the identification of preserved specimens, as they show some overlap among the species. Other morphological characters also show statistical differences among the species (relative carapace length, major chela shape, female uropod spine shape) but there is so much overlap that the characters are of little help in identifying particular specimens.

The host, depth, and geographic region from which a shrimp is collected also provide some guidance as to the likely identity of the individual when morphological and color data are ambiguous. *Alpheus roquensis* has the most distinctive pattern, by virtue of its association with *H. lucida* and its apparently restricted (although incompletely known) geographic distribution. The three *Bartholomea* associates also show some ecological differences. *Alpheus immaculatus* is more common in 1) exposed environments (e.g., the forereef and coastal areas lacking a well developed reef crest) and 2) environments deeper than 13 m, including

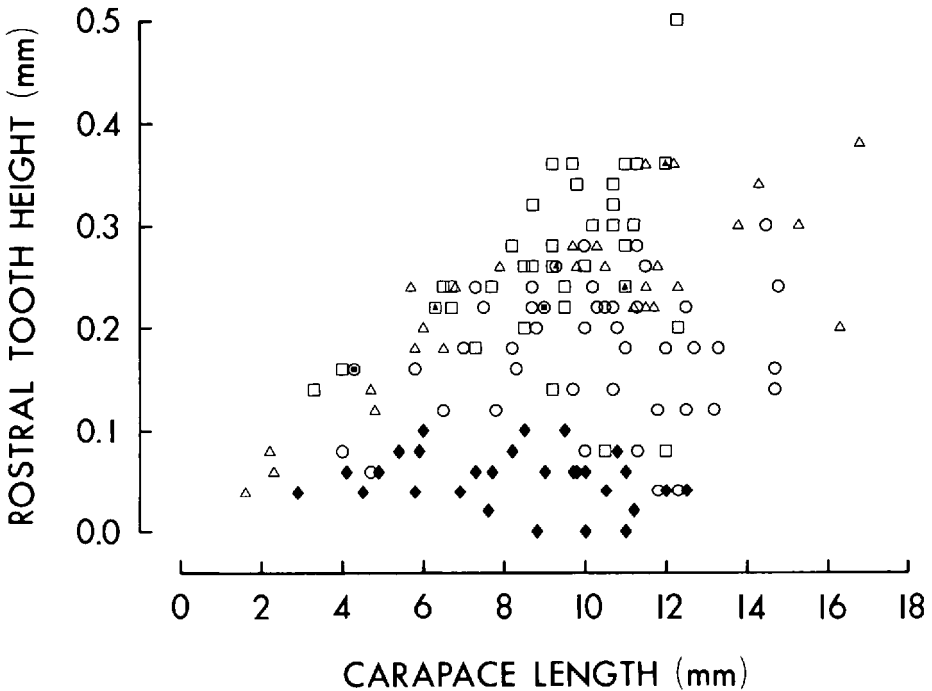


Figure 3. Relative height of post-rostral tooth. *Alpheus roquensis* (solid diamonds) overlaps little with the other three species (open symbols: circles—*A. armatus*, squares—*A. immaculatus*, triangles—*A. polystictus*) in this character. In *A. roquensis* it was often so reduced as to be simply a raised area rather than a tooth. In all specimens of this species it was less than 0.1 mm in height (vs. 13% of specimens in *A. armatus*, 5% in *A. immaculatus*, and 9% in *A. polystictus*).

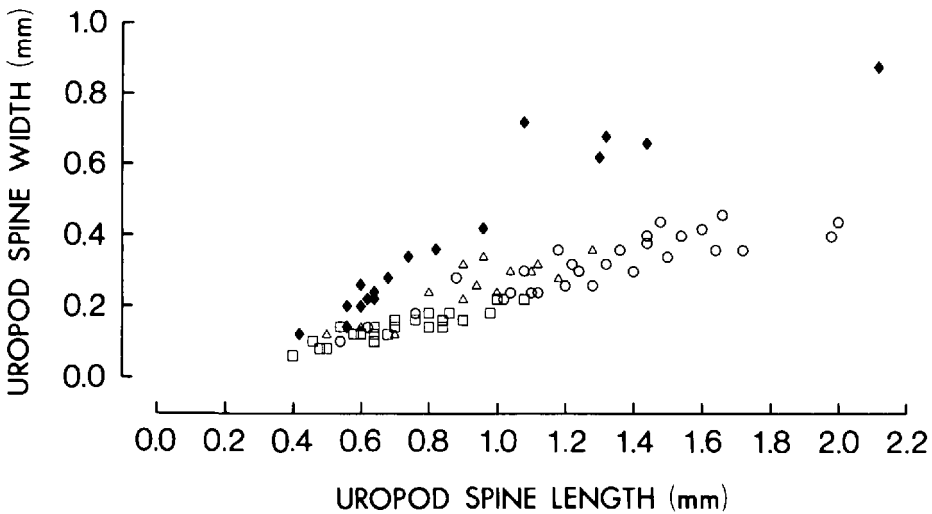


Figure 4. Shape of right uropod spine in males. Males of *A. roquensis* (solid diamonds) have proportionately broader uropod spines than the other three species (open symbols, see Fig. 3 for key). Width was measured at the point of insertion into the uropod, while length was measured along the midline from the point of insertion to the spine tip (see Fig. 5 for uropod illustration).

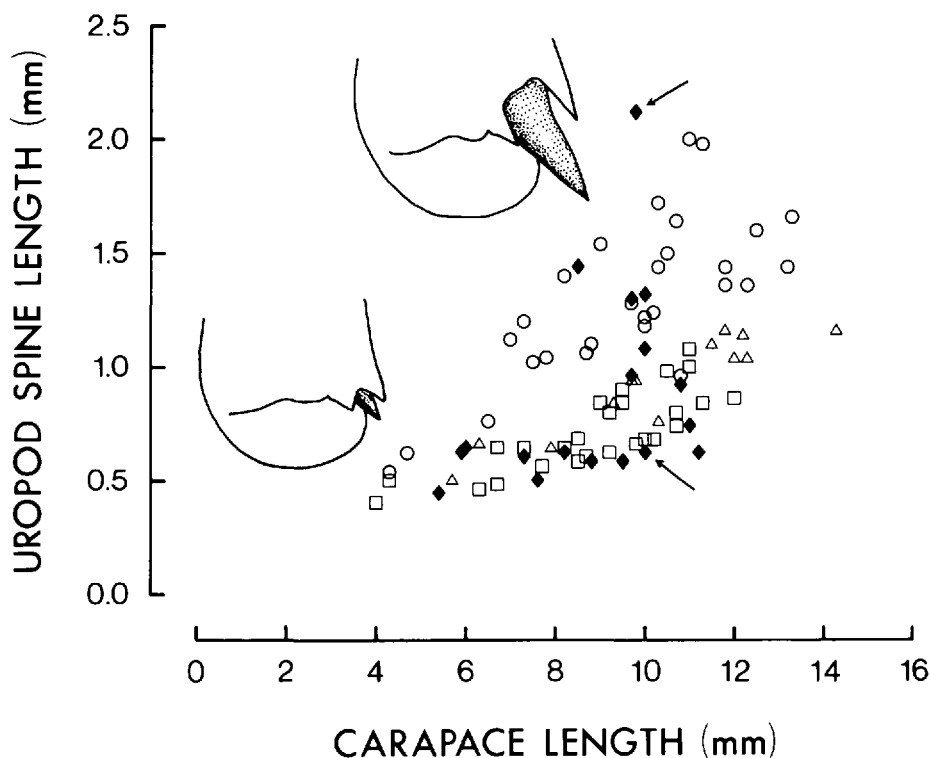


Figure 5. Relative length of right uropod spine in males. Males of *A. roquensis* (solid diamonds) show extreme variability in relative spine length, exceeding the range exhibited by the other three species combined (open symbols). The terminal portions of the right outer uropods from two comparably sized shrimp with grossly different uropod spines are illustrated, with arrows indicating the points which represent these individuals (upper arrow refers to upper uropod). There is no significant correlation between carapace length and uropod spine length in *A. roquensis* (regression analysis, $P = 0.127$), while for each of the other three species the regression is highly significant (P 's < 0.001). Drawings of outer uropods from two *A. roquensis* individuals of comparable size illustrate this variability. In addition, *A. armatus* (open circles) does not overlap with *A. immaculatus* (open squares) and *A. polystictus* (open triangles) in relative spine length, and can be distinguished from *A. roquensis* by its proportionately narrower spines (Fig. 4).

deep, protected areas. Both *A. armatus* and *A. polystictus* are most common in shallow protected areas (e.g., shallow, backreef lagoons). On a larger geographic scale, *A. polystictus* is rare in the northern Caribbean, but both species can be abundant in the southern Caribbean. However, the fact that shrimp are sometimes found in non-typical environments and regions, and occasionally with a non-typical host, makes the use of ecological data in species identifications problematic.

Evidence for Absence of Potential Interbreeding.—All four species live as male-female pairs, and mating occurs throughout the year approximately once every 3 weeks (Knowlton, 1980). Hence failure to find mixed-species pairs in the field can be taken as strong evidence for the absence of interbreeding. *A. roquensis* is reproductively isolated from the other three species by virtue of its association with a different species of anemone. The alpheid associates of *Bartholomea* also show no signs of interbreeding, for in areas where two or more of these species occur sympatrically, we have not observed a heterospecific male-female pair in

Table 2. Intraspecific vs. interspecific pairing behavior. Intraspecific pairing was routine, while interspecific pairing never took place ($\chi^2 = 45$, $P \ll 0.001$). For each sex both the total number of injured individuals and the number with serious injuries (multiple punctures or claw loss, in parentheses) are noted. Using either measure, injuries were much more likely to occur when shrimp of different species were placed in the same aquarium (χ^2 's = 40, 18; P 's $\ll 0.001$). Note that failure to form interspecific pairs with *A. roquensis* cannot be attributed to the effects of the presence of a non-host anemone for one of the species, since anemone species did not affect the outcomes

Shrimp	Anemone	Pairing		All injuries (serious)	
		Together	Separate	Female	Male
<i>A. arm.</i> × <i>A. arm.</i>	<i>B. annulata</i>	3	0	0	0
<i>A. arm.</i> × <i>A. arm.</i>	<i>H. lucida</i>	3	0	0	0
<i>A. imm.</i> × <i>A. imm.</i>	<i>B. annulata</i>	3	0	0	0
<i>A. imm.</i> × <i>A. imm.</i>	<i>H. lucida</i>	3	0	0	0
<i>A. pol.</i> × <i>A. pol.</i>	<i>B. annulata</i>	3	0	1 (0)	1 (0)
<i>A. pol.</i> × <i>A. pol.</i>	<i>H. lucida</i>	3	0	0	0
<i>A. roq.</i> × <i>A. roq.</i>	<i>B. annulata</i>	3	0	0	0
<i>A. roq.</i> × <i>A. roq.</i>	<i>H. lucida</i>	4	1	2 (1)	2 (0)
<i>A. arm.</i> × <i>A. imm.</i>	<i>B. annulata</i>	0	3	2 (2)	3 (1)
<i>A. arm.</i> × <i>A. pol.</i>	<i>B. annulata</i>	0	3	3 (1)	1 (1)
<i>A. arm.</i> × <i>A. roq.</i>	<i>B. annulata</i>	0	3	3 (2)	2 (2)
<i>A. arm.</i> × <i>A. roq.</i>	<i>H. lucida</i>	0	3	3 (0)	1 (0)
<i>A. imm.</i> × <i>A. pol.</i>	<i>B. annulata</i>	0	3	2 (0)	1 (1)
<i>A. imm.</i> × <i>A. roq.</i>	<i>B. annulata</i>	0	3	3 (2)	3 (0)
<i>A. imm.</i> × <i>A. roq.</i>	<i>H. lucida</i>	0	3	3 (3)	2 (2)
<i>A. pol.</i> × <i>A. roq.</i>	<i>B. annulata</i>	0	3	2 (1)	2 (1)
<i>A. pol.</i> × <i>A. roq.</i>	<i>H. lucida</i>	0	3	2 (0)	2 (1)

hundreds of collections (Knowlton and Keller, 1983). Even where one species is rare (*A. polystictus* in Discovery Bay, Jamaica, where it represents fewer than 1% of the pairs), one never finds a male or female paired with a member of one of the more common species. In addition, it is impossible to force pairings in the laboratory between species, while it is easy to do so when both individuals belong to the same species (Table 2). Finally, we have seen no apparent hybrids (i.e., individuals with ambiguous color patterns).

Host Preferences.—In the laboratory, shrimp of all four species are physically capable of sheltering under both *Bartholomea annulata* and *Heteractis lucida*, and as the mating experiments showed, they will even form pairs under an anemone which is not their normal host. Thus the very tight association of a shrimp species with a single anemone species in the field could be due to either host preference or to competitive exclusion. The results of laboratory experiments on host preferences indicate that the former is at least partly responsible for the field pattern, as the shrimps showed strong (although not generally perfect) preferences for the anemone species from which they were collected (Table 3). More and longer experimental observations are needed, however, to determine whether the species differ in the strength of their preferences and whether preferences can be shifted by experience.

DISCUSSION

The four species of alpheid shrimp associated with the sea anemones *Bartholomea annulata* and *Heteractis lucida* are clearly closely related. They are very similar morphologically and in many aspects of their color pattern (Fig. 1), and

Table 3. Host preferences of the four shrimp species. Shrimp were introduced to either *B. annulata* (host for *A. armatus*, *A. immaculatus* and *A. polystictus*) or *H. lucida* (host for *A. roquensis*) in an aquarium containing both anemone species. Introduction to a non-host anemone was significantly more likely to result in movement by the shrimp to the other anemone species than was introduction to a host anemone (two-tailed Fisher exact probability test: *A. armatus*, $P = 0.003$; *A. immaculatus*, $P = 0.0007$; *A. polystictus*, $P < 0.0001$; *A. roquensis*, $P = 0.028$)

Shrimp spp.	Host		Non-host	
	Change	No change	Change	No change
<i>A. armatus</i>	2	6	10	0
<i>A. immaculatus</i>	0	8	8	1
<i>A. polystictus</i>	0	10	10	0
<i>A. roquensis</i>	3	8	9	2
All	5	32	37	3

preliminary electrophoretic studies (in preparation) also suggest a recent separation. Unfortunately, the characters which most readily distinguish the four species, mating preferences and relatively minor color differences, cannot be used with preserved specimens. There may be many undescribed sibling species among the Crustacea, and they will be easiest to discover in species which live in male-female pairs (many symbiotic species; Bruce, 1976).

The mechanisms responsible for speciation in this group remain unclear. Although considerable attention has been drawn to the possibility of speciation associated with changes in host (Bush, 1975), three of these sibling symbiotic species share the same host. Interestingly, the most distinctive species ecologically (*A. roquensis*) does not appear to be comparably distinctive in color pattern. There appear to be similar groups of closely related, sympatric species sharing the same host among some of the symbiotic crabs and shrimp of the Pacific (Patton, 1966; Preston, 1973; Bruce, 1975; 1978; Glynn, 1983; Huber, 1985a; 1985b). These taxa may be particularly amenable to further investigations of mechanisms of speciation.

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NOTE ADDED IN PROOF: We have seen no *A. roquensis* during preliminary surveys of *Heteractis lucida* in Panama.

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